

Cephalic Morphology of *Ariosoma gilberti* (Bathymyrinae: Congridae)

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Abstract: The head bones and relevant muscles are important elements composing the feeding and respiration apparatus and can be considered as highly important structures for giving rise to evolutionary specializations. The eels of the Anguilloidei is a diverse group and structural diversity in their cranial musculoskeletal system is thus to be expected. *Ariosoma gilberti* is a member of Bathymyrinae (Congridae) with a hydraulic based prey transport and closely related to muraenid family with mechanical prey transport system. Since there is no information about the cephalic morphology of *A. gilberti*, hence this study was conducted to provide detailed description of its cranial osteology and myology. The immobile maxillary with large pointed teeth, an anterior moderate mouth gape, large jaw closing muscles and large lateral and ventral bony elements, providing more room for the orobranchial cavity of *A. gilberti* suggesting the presence of a hydraulic and suction-based mechanism.

Keywords: Anguilliform, Osteology, Myology, Cranial morphology, Adaptation.

Introduction

The head musculoskeletal system and its integration in the functioning of the skull can be considered as a highly important pattern for giving rise to evolutionary specializations by means of natural selection. The head of fishes is quite complex, with over 30 individual bony elements that can be moved by their associated muscles. Throughout evolution, quite some variation originated in the cranial musculoskeletal system of fishes. Judging from that, it can be expected that many combinations of muscles and bones are possible to perform a certain function, such as those for mouth opening and closing. The head bones and relevant muscles are important elements composing the feeding and respiration apparatus.

The eels of the Anguilloidei are a suborder comprising fifteen families, thereby forming the richest suborder within the Elopomorpha (Nelson 2006). This suborder still needs to be fully explored. Many new species of Anguilliformes are described

each year (Smith & Kanazawa 1977; Castle & McCosker 1999; Chen & Mok 2001; Smith and Karmovskaya 2003; Smith 2004), and more are expected to be recognized as various habitats are examined more closely, especially those of the deep seas. The diversity of eels is astounding and structural diversity in their cranial musculoskeletal system is thus to be expected. The study of such a diversity will provide information on how their structures have changed through adaptive (or non-adaptive) evolution and this may contribute to a better understanding of Anguilliformes classification and evolution.

The Congridae is one of the largest and most divers anguilliform family (Smith 1989). This family comprises three subfamilies (Heterocongrinae, Bathymyrinae and Congrinae) with 32 genera and roughly 160 species (Nelson 2006). The Congridae are found worldwide in tropical and subtropical latitudes and occur in the Atlantic, Pacific and Indian Oceans. *Ariosoma gilberti* is a member of

Bathymyrinae with a hydraulic based prey transport system and form a monophyletic clade with Muraenidae with a mechanical prey transport system (Mehta & Winwright 2007), based on mitochondrial 12S ribosomal RNA sequences (Obermiller & Pfeiler 2003). Hence, comparison of Bathymyrinae and Muraenidae belonging to a monophyletic group with a single evolutionary origin of an eel-like body, provides an opportunity to better understand the evolutionary changes in the cranial musculoskeletal system, of which, some are the adaptations to different modes of life. Since there is no information about the cephalic morphology of *A. gilberti*, we provide a detailed description of its cranial myology and osteology and attempt to compare it with those of muraenids published in Mehta & Winwright (2007) and Eagderi (2010). The cranial osteology and myology of *Gymnothorax prasinus* and *Anarchias allardicei* (Muraeninae and Uropterygiinae: Muraenidae) were described in details by Eagderi (2010). The results of this study can help to better understand the morphological changes of the head that have occurred during evolution toward mechanical based prey transport system.

Material and methods

For the anatomical description, two specimens of *Ariosoma gilberti* (UF 230612, 133 mm TL and UF 10803, 182 mm TL), obtained from the Florida Museum of Natural History, were examined. The two specimens were cleared and stained with Alizarin red S and Alcian blue according to the protocol of Hanken & Wassersug (1981) for osteological examinations. Dissections with muscle fiber staining were performed according to Bock & Shear (1972). Specimens were studied using a stereoscopic microscope (Olympus SZX-7) equipped with a camera lucida.

The musculature terminology follows Winterbottom (1974), De Schepper et al. (2005) and Mehta & Wainwright (2007). The circumorbital bones of the cephalic lateral line system follow

Adriaens et al. (1997) terminology. Terminology of cranial skeletal elements follows Nelson (1966), Böhlke (1989) and Rojo (1991). The epiotic of teleosts is termed "epioccipital", thereby following Patterson (1975). The terminology of scarf joint follows Hildebrand (1995).

Results

Cranial osteology: The neurocranium forms one unit, tapering from the otic region towards the anterior end of the frontal bone and then continuing as a narrow bar towards the spatulate-like snout (Fig. 1a). The ethmoid region comprises the fused premaxillaries, ethmoid and vomeral bones, as the premaxillo-ethmovomer complex and nasals. The nasal bone is described with respect to the lateral line system (see below). The premaxillo-ethmovomer complex bears a lateral process, which is directed anteroventrally with a small horizontal process at its end (Figs. 1 and 2a) and the olfactory rosette is located anterior to this process. The anteroventral face of the premaxillo-ethmovomer complex is dentigerous with anterior, longer and recurved caniniform teeth (Fig. 1b).

The orbital region comprises the two small lacrimal bones, four infraorbital bones, frontal bones, parasphenoid, basisphenoids and pterospheoids. Posteriorly, the frontal bones are connected with the parietal bones by an extensive scarf joint (Fig. 1a). Also, left and right frontal bones show a minor scarf joint (Fig. 1a). The ventroposterior rim of the frontal bone encloses the anterior portion of the temporal canal, which enters this bony canal at the connection between the frontal and pterospheoid (Fig. 2a). The frontal forms the posterodorsal wall of the large orbit, and the foramen opticum lies between the ventral portions of the frontal bones. Anteriorly, the frontal bears a small lateral process over the orbit with a pore on its posterior part. The basisphenoid forms the posteroventral wall of the orbit and bears a small fossa on its anteroventral face. The dorsal part of this bone runs into the optic foramen and overlaps

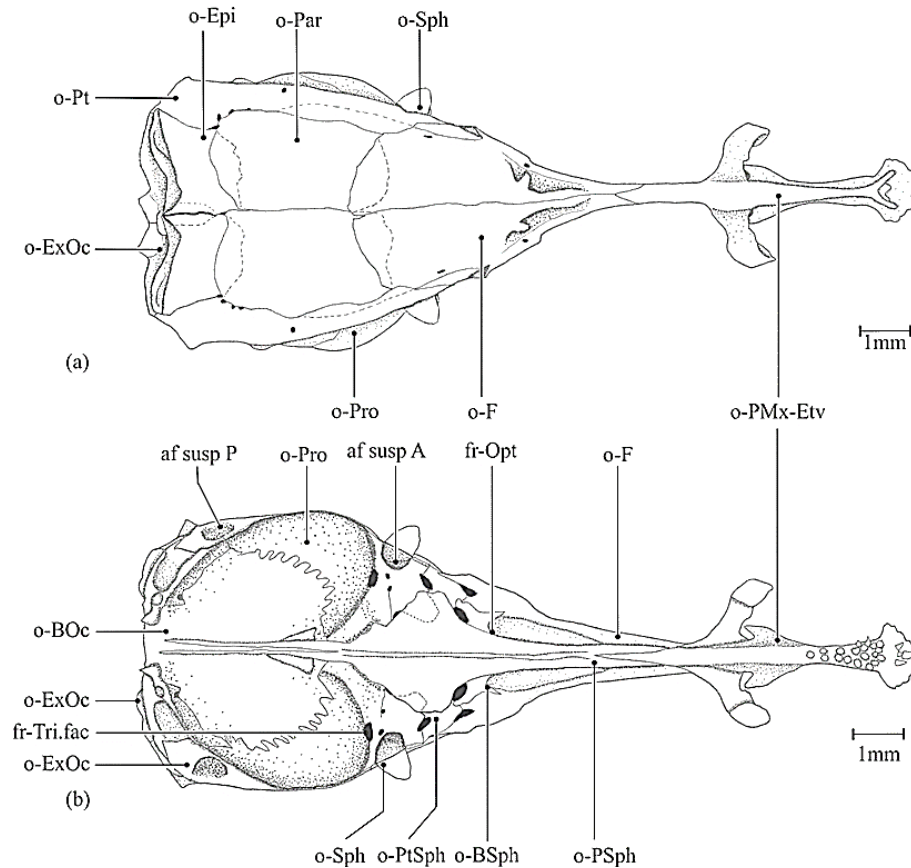


Fig.1. Neurocranium of *Ariosoma gilberti*. (a) Dorsal view and (b) ventral view. af susp A, anterior suspensorial articulation facet; af susp p, posterior suspensorial articulation facet; fr-Opt, foramen opticum; fr-Tri.fac, foramen trigemino-facialis; o-BOc, basioccipital bone; o-BSph, basisphenoid; o-Epi, epioccipital bone; o-ExOc, exoccipital bone; o-F, frontal bone; o-Par, parietal bone; o-PMx-Etv, premaxillo-ethmovomer complex; o-Pro, prootic bone; o-PSph, parasphenoid; o-Pt, pterotic bone; o-PtSph, pterosphenoid; o-Sph, sphenotic bone.

ventrally with the parasphenoid. The pterosphenoid is surrounded by the frontal, basisphenoid, parasphenoid, sphenotic and prootic bones. The pterosphenoid possesses a pore on its lateral face (Fig. 2a). The parasphenoid is bifurcated at its two ends and forms the ventral element of the orbit. At the midpoint, the parasphenoid bone bears distinct alar processes as well as a ventral keel (Fig. 1b). The otic region is comprised of the sphenotics, pterotic, prootics, parietals and epioccipitals. The sphenotic is connected to the prootic bone by a bony strut of the prootic. The sphenotic contributes to form the anterior suspensorial articulatory facet, together with the prootic bone (Figs. 1b and 2a). The sphenotic bone bears a lateral process directing vertically. The pterotic bone braces the neurocranium laterally and encloses the posterior portion of the temporal canal,

which opens at the posterodorsal face of the pterotic (Figs. 3a). Posteriorly, this bone connects to the exoccipital bone and contributes to form the posterior wall of the neurocranium. The posterior articulatory facet for the hyomandibula is formed by the pterotic bone (Fig. 1b). The large prootic forms the anterior part of the otic bullae, with the foramen trigemino-facialis at the anterior edge of the bulla and two pores anterior to this foramen (Fig. 1b). The prootic possesses a long dorsal projection on its anterodorsal corner that runs under the posterior portion of the frontal. The anterior part of the parietal is covered by the frontal bone forming a relatively extended scarf joint.

The occipital region consists of the exoccipital and basioccipital bones. A supraoccipital is absent. Both exoccipital bones are interconnected

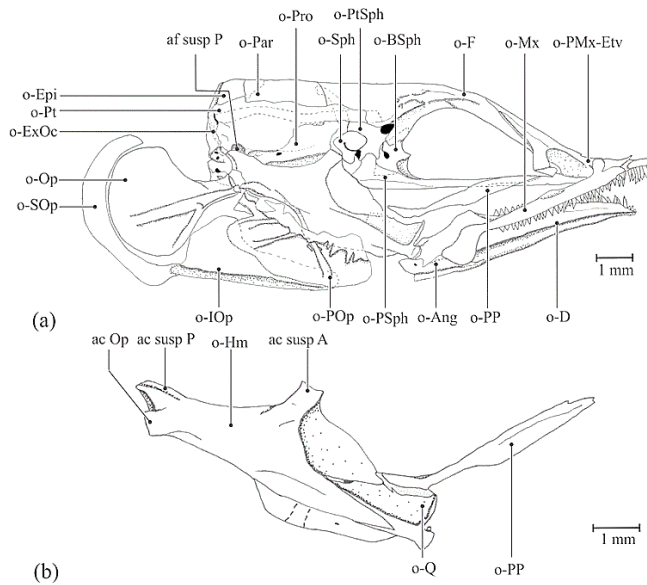


Fig.2. Cranial skeleton of *Ariosoma gilberti* (Lateral view). (a) Complete skull (right side) and (b) suspensorium (right side). ac Op, opercular articular condyle; af susp p, posterior suspensorial articulation facet; ac susp A, anterior suspensorial condyle; ac susp P, posterior suspensorial condyle; o-Ang, angular bony complex ; o-BSph, basisphenoid bone; o-D, dentary complex; o-Epi, epioccipital bone; o-ExOc, exoccipital bone; o-F, frontal bone; o-Hm, hyomandibular bone; o-Iop, interopercle; o-Mx, maxillary bone; o-Op, opercle; o-Par, parietal bone; o-PMx-Etv, premaxillo-ethmovomer complex; o-POp, preopercle; o-PP, palatopterygoid; o-Pro, prootic bone; o-PSph, parasphenoid; o-Pt, pterotic bone; o-PtSph, ptersphenoid bone; o-Q, quadrate; o-SOp, subopercle; o-Sph, sphenotic bone.

posterodorsally. The exoccipital bones ventrally form a depression on the posteroventral face of the neurocranium (Fig. 1b). The foramen magnum is bordered dorsally and laterally by the exoccipitals and ventrally by the condyle of the basioccipital. The basioccipital forms the posterior portion of the large otic bullae and wedges into the long posterior incisure of the parasphenoid.

The lower jaw ventrally forms a long groove, enclosed deep internal wall and shorter external wall, which supports the anterior part of the preoperculo-mandibular canal (Figs. 2a and 3a). The anterior portion of the lower jaw represents the dento-spleno-mentomeckelian complex, here referred to as the dentary complex. The dentary complex posterodorsally bears the coronoid process with a

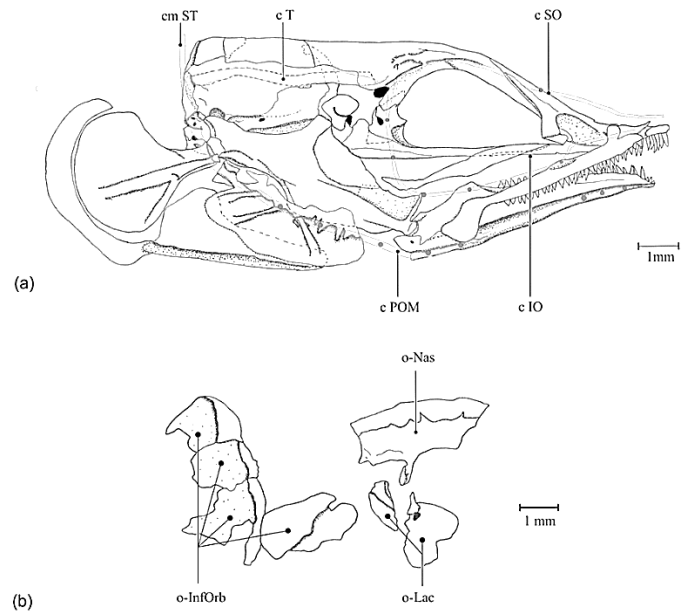


Fig.3. The cranial lateral line system of *Ariosoma gilberti*. (a) position of the composing canals in relation to the skull (right side, lateral view) and (b) lateral view of the nasal bone, lacrimal bones and infraorbital bones (right side) (relative position of bones do not correspond to their real position). c IO, infraorbital canal; c POM, preopercular mandibular canal; c SO, supraorbital canal; c T, temporal canal; cm ST, supratemporal commissure; o-Nas, nasal bone; o-InfOrb, infraorbital bone; o-Lac, lacrimal bone.

small coronomeckelian bone ventral to the process and bearing an apophysis on its medial face (Fig. 4b). The anterior portion of the coronomeckelian is enclosed by the dentary complex. A small meckelian fossa is present at the rear of the coronomeckelian (Fig. 4b). Anteriorly, the dentary teeth are arranged in three rows and posteriorly in two rows of teeth with their tips pointing medially. The angular complex consists of the fused angular and articular bones, bearing a small retroarticular process (Fig. 4b). This complex wedges into the dentary complex. The retroarticular process is directed caudally and bears a pore. The opening of a canal is present anterior to the retroarticular process and anteriorly this canal opens into the posterior part of the meckelian fossa (Fig. 4b). Also, there is a small pore on the medial face of this canal. The angular complex bears the caudodorsally directed mandibular articular facet. In the upper jaw, the

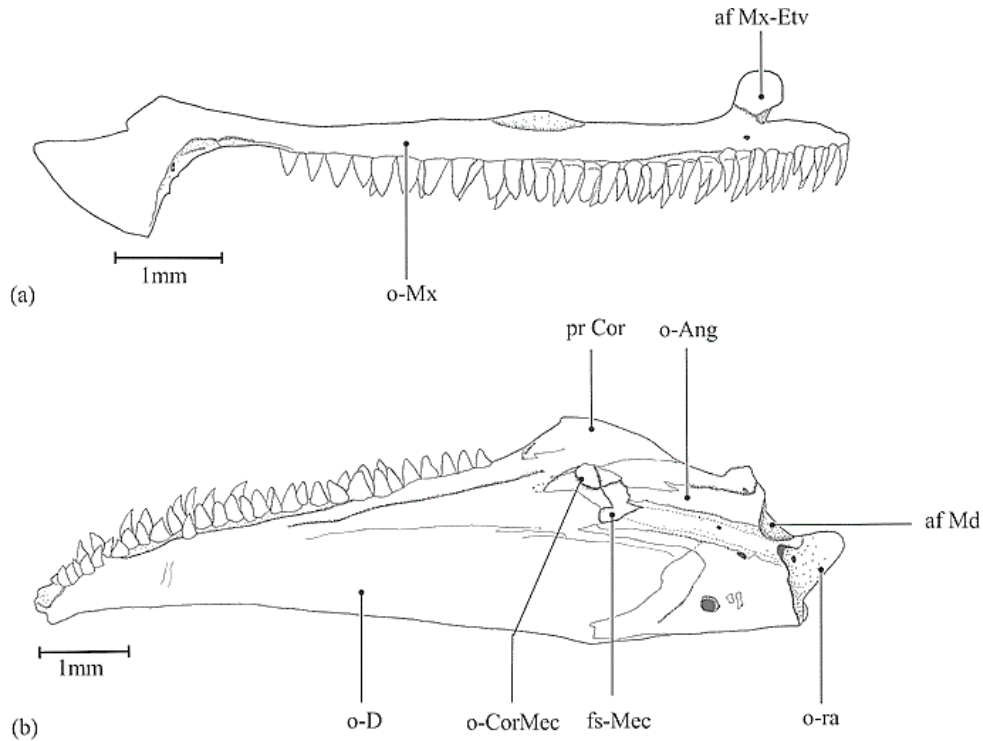


Fig.4. Jaws of *Ariosoma gilberti* (right side) (a-b), maxillary; medial view (a), and lower jaw; medial view (b). af Md, mandibular articulation facet; af Mx-Etv, maxillo-ethmovomer al articular facet; o-Ang, angular bony complex ; o-D, dentary complex; o-Mx, maxillary bone; o-CorMec, coronomeckelian bone; fs-Mec, meckelian fossa; pr Cor, coronoid process; o-ra, retroarticular bone.

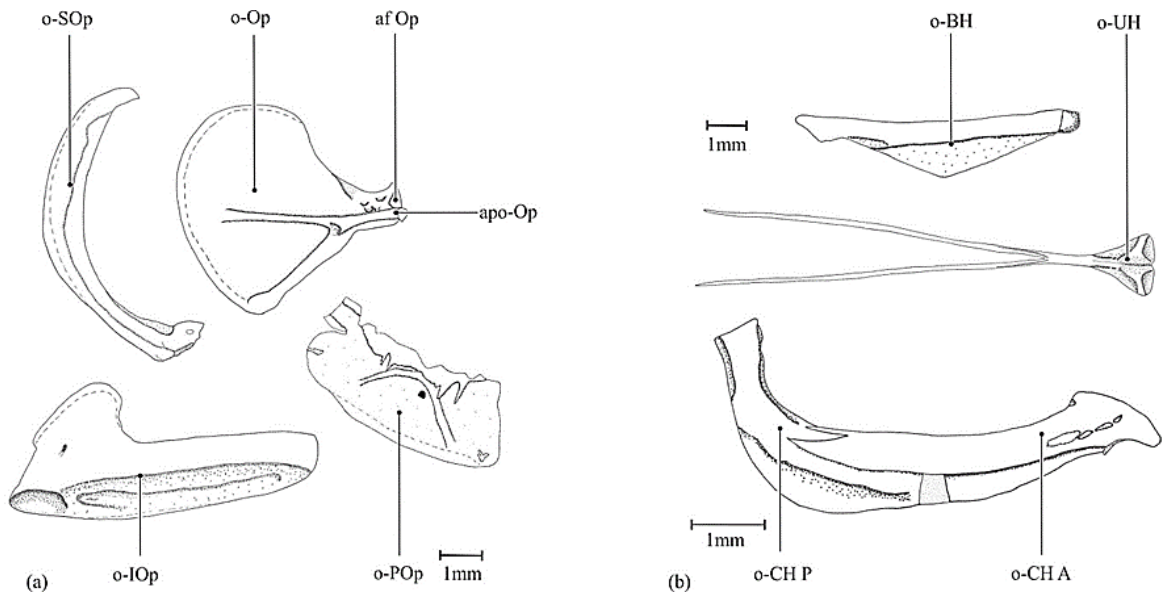


Fig.5. Opercular series and hyoid apparatus of *Ariosoma gilberti*. (a) Opercular series; lateral view (right side) and (b) hyoid apparatus; lateral views of the anterior ceratohyal and posterior ceratohyal bones, dorsal views of urohyal, and lateral view of basihyal (right side). af Op, opercular articular facet; apo-Op, apophysis of opercle; o-BH, basihyal bone; o-CH A, anterior ceratohyal bone; o-CH P, posterior ceratohyal bone; o-IOP, interopercle; o-Op, opercle; o-POp, preopercle; o-SOp, subopercle; o-UH, urohyal bone.

maxillary bone is attached anteromedially to the premaxillo-ethmovomer al complex via an ascending

articular process that is situated at the rear of its anterior end (Figs. 2a and 4a). Anteriorly, the

maxillary bone bears a patch of pointed teeth and posteriorly a double row of curved and pointed ones with a few posterior teeth that are arranged in a single row. The posterior end of the maxillary bone descends ventrally and is connected to the angular complex via the primordial ligament.

The suspensorium is comprised of four bones including the hyomandibula, quadrate, palatopterygoid and preopercle. The preopercle is described as part of the opercular series (see below). The suspensorium is longer than deep and bears an anterior fossa that is formed by the anterior portions of the hyomandibula and quadrate (Fig. 2b). The palatopterygoid anteriorly connects to the anterior part of the parasphenoid (Fig. 2a). There is a large synchondrosis at the connection of the palatopterygoid to the suspensorium. The hyomandibula is firmly connected to the quadrate with an interdigitated suture. The axis of the hyomandibula-quadrate inclines forwardly, placing the quadrate-mandibular joint at the level of the posterior part of the orbit (Fig. 2a). The hyomandibula bears three articular condyles: an anterior one articulating with the sphenotic and prootic; a posterior one articulating with the pterotic; and the opercular condyle situated at the posterodorsal margin of the hyomandibular bone (Fig. 2b). A distinct symplectic was not observed.

The opercular series consists of four bones: the preopercle, interopercle, subopercle and opercle (Fig. 5a). The distal margins of the opercular and subopercle bones were lightly stained in the specimen studied. The ventromedial face of the preopercle is connected to the posteroventral rim of the suspensorium. The entire anterolateral face of the preopercle forms a tubular structure that encloses the posterior portion of the preopercular-mandibular canal (Figs. 3a and 5a). The posterior rim of the preopercle covers the anterior margin of the interopercle. The ventral face of the interopercle curves medially and its anteromedial edge is connected to the angular bony complex by the interoperculo-angular ligament. The subopercle lies

curved against the entire posterior margin of the opercle. The fan-shaped opercle articulates through its rostral process to the hyomandibular bone. Two ridges are present on the lateral face of the opercle, anteriorly forming an apophysis at the anterolateral face of the opercular rostrum.

The hyoid complex is comprised of the unpaired basihyal and urohyal, paired anterior and posterior ceratohyals (Fig. 5b). The rod-like basihyal bone bears a ventral crest that is connected to the lateral face of the anterior ceratohyal bone by the basihyaloceratohyal ligament. Anteriorly, the urohyal bone bears a deep and thick portion with a cross-like ridge on its dorsal face that forms the left and right ceratohyal articular facets. Posteriorly, the urohyal forms a brace-like part that bears two long processes (Fig. 5b). The anterior ceratohyal is firmly connected to the posterior one. The anterior ceratohyal ventromedially bears the urohyal articular condyle and dorsomedially the basihyal articular condyle. The posterior part of the posterior ceratohyal curves dorsally and is connected to the posteroventral corner of the angular complex by the ceratohyalangular ligament. Four of the eleven branchiostegal rays are connected to the anterior ceratohyal, the others to the posterior ceratohyal. The branchiostegal rays curve dorsally along the ventral border of the interopercle and reach up to the caudal border of the subopercle.

The cephalic lateral line system is comprised of the supraorbital, infraorbital, temporal and preoperculo-mandibular canals, and supratemporal commissure. The ethmoid canal, adnasal canal and frontal commissure were not observed. The supraorbital canal extends over the olfactory rosette to the postorbital region and possesses a single external pore. The anterior openings of the left and right supraorbital canals abut (Fig. 3a). The nasal bone is a rectangular bone with a ventral process at its midpoint (Fig. 3b). Dorsally, it bears a tubular structure that supports the anterior portion of the supraorbital canal (Fig. 3b). This bone was also

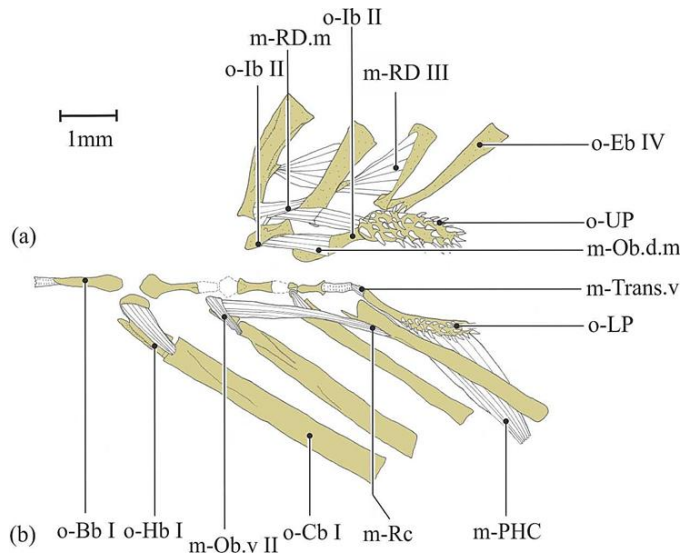


Fig.6. Gill arches and associated muscles of *Ariosoma gilberti*. (a) Dorsal view of the ventral part and (b) ventral view of the dorsal part of the gill arch. o-Bb, basibranchial bone; o-Cb, ceratobranchial bone; o-Eb, epibranchial bone; o-Hb, hypobranchial bone; o-Ib, infrapharyngobranchial bone; o-LP, lower pharyngeal tooth plates; o-UP, upper pharyngeal tooth plates; m-Ob.d.m, medial obliquus dorsalis muscle; m-Ob.v, ventral obliquus dorsalis muscle; m-PHC, pharyngocleithralis muscle; m-Rc, rectus communis muscle; m-RD, rectus dorsalis muscle; m-RD.m, medial rectus dorsalis muscle; m-Trans.v, transversus ventralis muscle.

slightly stained. The infraorbital canal starts at the rear of the snout tip. This canal extends posteriorly and curves dorsally into the postorbital region and anastomoses with the supraorbital canal in front of the entrance of the temporal canal into the skull (Fig. 3a). Two lacrimal bones support the anterior part of the infraorbital canal and its posterior part is enclosed by four infraorbital bones before anastomosing with the supraorbital canal (Fig. 3b). The infraorbital canal bears five external pores. The temporal canal runs inside the frontal and pterotic bones. The preoperculo-mandibular canal starts from the tip of the dentary complex and runs in the ventral groove of the mandibula. This canal continues into the tubular part of the preopercle and anastomoses with the posterior end of the temporal canal (Fig. 3a). The preoperculo-mandibular canal bears nine external pores.

Almost all ventral elements of the branchial arches are present (Fig. 6): Four basibranchial bones (Bb I-VI), two pairs of hypobranchial bones (Hb I-II) (the third pair is smaller and unossified), five pairs of ceratobranchial bones (Cb I-V) (fifth pair is reduced, located ventrally to the pharyngocleithralis muscle), and one pair of lower pharyngeal tooth plates (LP). The dorsal elements of the gill arches present are: Four pairs of epibranchial bones (Eb I-IV), two pairs of the infrapharyngobranchial bones and one pair of the upper pharyngeal tooth plates (UP) (Fig. 6). The upper and lower tooth plates bear small teeth, pointing caudally.

Cranial Myology: The adductor mandibulae muscle complex comprises the sections A2 and A3. The section A2 can be subdivided into three subsections: A2 α , A2 β anterior (A2 β a) and A2 β posterior (A2 β p) (Fig. 7a). The lateral fibers of the subsection A2 β a originate musculosly from the epioccipital, pterotic, parietal and posterior part of the frontal, its medial fibers originating musculosly from the anterior part of the sphenotic process. This subsection inserts as a tendon onto the anteromedial face of the coronoid process. The posterodorsal fibers of A2 β p are attached to their counterpart and fascially to the epaxial, and originate musculosly from the epioccipital, pterotic and parietal. The lateral fibers, together with the lateral fibers of the subsection A2 α , are connected to the tendon A2 that inserts on the posteromedial face of the coronoid process. The medial fibers of A2 β p also insert musculosly on the posteromedial edge of the coronoid process. The lateral fibers of the A2 α originate musculosly from the preopercle, hyomandibula and quadrate bones. Its medial fibers originate musculosly from the lateroposterior face of the hyomandibula and the ventroposterior edge of the suspensorial fossa. They insert musculosly on the posteromedial face of the mandibula from the Meckelian fossa to the anterior edge of the retroarticular process.

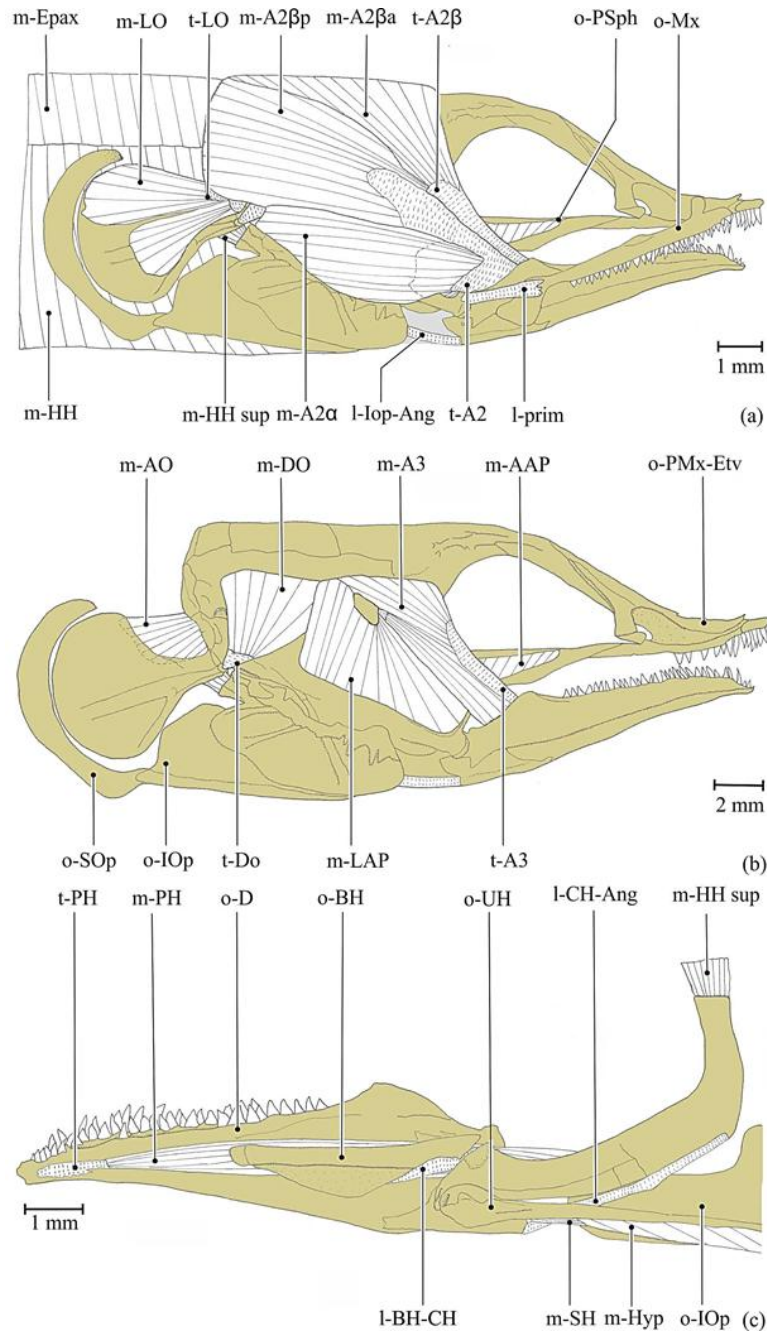


Fig.7. The cranial muscles of *Ariosoma gilberti*. (a) Skin removed (lateral view), (b) sections A2, hyohyoideus muscle complex, epaxial muscles, hypaxial muscles, ventral muscles of the head, branchiostegal rays and primordial ligament are removed (lateral view) and (c) ventral muscles of head (sagittal left cut), hyohyoideus muscle complex is removed and (d) Position of the muscles on the medial face of the suspensorium. l-CH-Ang, ceratohyalo-angular ligament; l-BH-CH, basihyalo-ceratohyal ligament; l-Iop-Ang, interoperculo-angular ligament; l-prim, primordial ligament; m-A2 α , ventral subsection of A2; m-A2 β a, anterior part of dorsal subsection of A2 β ; m-A2 β p, posterior part of dorsal subsection of A2 β ; m-A3, A3 section of the adductor mandibulae muscle complex; m-AAP, adductor arcus palatini muscle; m-AO, adductor operculi muscle; m-DO, dilatator operculi muscle; m-Epax, epaxial muscles; m-HH, hyohyoideus muscle complex; m-HH sup, hyohyoideus superior muscle; m-Hyp, hypaxial muscles; m-LAP, levator arcus palatini muscle; m-LO, levator operculi muscle; m-PH, protractor hyoidei muscle; m-SH, sternohyoideus muscle; o-BH, basihyal bone; o-D, dentary complex; o-Iop, interopercle; o-Mx, maxillary bone; o-PMx-Etv, premaxillo-ethmovomer complex; o-PSph, parasphenoid bone; o-Sop, subopercle; o-UH, urohyal bone; t-A2, tendon of A2; t-A2 β , tendon of A2 β ; t-A3, tendon of A3; t-DO, tendon of dilatator operculi muscle; t-LO, tendon of levator operculi; t-PH, tendon of protractor hyoidei.

The section A3 originates musculously from the ventral part of the frontal, pterospheoid and anterior part of the prootic, and tendinously from the anteroventral face of the sphenotic process (Fig. 7b).

The anterior fibers of this muscle insert tendinously on the ventromedial face of the coronoid process, at the rear of the insertion point of the tendon A2 β . Its posterior fibers insert onto the dorsal face of the Meckelian fossa.

The adductor arcus palatini is a thin muscle that originates musculously from the ventral keel of the parasphenoid (Fig. 7b). This muscle inserts musculously on the laterodorsal face of the palatopterygoid and anteromedial face of the hyomandibula. Its posterior fibers merge with the anteromedial fibers of the adductor hyomandibulae.

The adductor hyomandibulae is distinguished from the adductor arcus palatini due to its thicker diameter. This muscle originates musculously from the anterior part of the basioccipital, pterotic and prootic and inserts musculously on the ventromedial face of the hyomandibula and quadrate.

The levator arcus palatini is situated posterior to the section A3 of the adductor mandibulae muscle complex (Fig. 7b). It originates musculously from ventral face of the sphenotic process, lateral face of the prootic and posterior face of the parasphenoid alae and inserts musculously on the lateroventral face of the suspensorial fossa and the laterodorsal face of the hyomandibular body.

The levator operculi comprises a ventral and a dorsal bundle (Fig. 7a). The ventral bundle originates tendinously from the posterodorsal depression of the hyomandibula that is situated dorsal to the opercle articular condyle and inserts musculously on the ventrolateral face of the opercle. The dorsal bundle originates tendinously from the lateroventral face of the exoccipital and inserts musculously on the dorsolateral face of the opercle (Fig. 7a).

The adductor operculi muscle originates musculously from a ventral depression on the exoccipital and the posterolateral face of the

basioccipital. It inserts on the dorsomedial rim of the opercle. The lateral fibers of this muscle merge with the medial fibers of the dorsal bundle of the levator operculi (Fig. 7b).

The dilatator operculi is a triangular muscle that is situated posterior to the levator arcus palatini (Fig. 7b). It originates musculously from the lateral face of the prootic and ventral face of the pterotic and inserts tendinously onto an apophysis on the anterolateral face of the rostral opercular process (Fig. 7b).

The protractor hyoidei muscle connects the posterior ceratohyal to the lower jaw. Each half (right and left) of this muscle originates tendinously from the medial face of the dentary bone at the rear of its symphysis and inserts tendinously on the lateral face of the posterior ceratohyal (Fig. 7c).

The sternohyoideus muscle inserts as a tendon on the anterior thicker part of the urohyal and musculously on the medial faces of two posterior processes of the urohyal (Fig. 7c). The ventral fibers of the sternohyoideus, which insert on the anteromedial faces of the posterior processes of the urohyal, merge with the ventral extended fibers of the hypaxials. The dorsal fibers of the sternohyoideus, which insert on the entire medial faces of the posterior processes of the urohyal, are divided posteriorly into two bundles and originate from the lateral face of two cleithra.

The hyohyoideus superior muscle connects the posteromedial edge of the posterior ceratohyal to the medial margin of the rostral opercular process (Fig. 7c).

The hyohyoideus muscle complex (presumably an undifferentiated complex of the hyohyoideus inferioris and hyohyoidei adductors) is a muscle sheet that lies between the medial faces of the branchiostegal rays and forms a thin sac-like muscle meeting its counterpart at the ventral midline (Fig. 7a). The anterodorsal fibers of this muscle attach on the medial face of the opercle and posterodorsally on the horizontal septum between the epaxial and hypaxial muscles, by connective tissue.

The muscles serving the ventral parts of the branchial arches consist of the pharyngocleithralis (PHC), three pairs of the obliqui ventrales (Ob.v I-III), rectus communis (RC) and transversus ventralis of the lower tooth plates (Trans.v). The pharyngocleithralis muscle connects the lower tooth plate to the cleithrum (Fig. 6). The obliquus ventralis spans the ceratobranchial-hypobranchial joint of the first three branchial arches. The rectus communis connects the posterodorsal face of the second hypobranchial to the fourth ceratobranchial. The transversus ventralis tendinously connects the pharyngeal lower tooth plates to the posterior end of the fourth basibranchial (Fig. 6). The rectus dorsalis I-II (RD I: connects the first and second epibranchial; RD II: connects the second and third epibranchial), medial rectus dorsalis (RD.m; interconnects first and second epibranchial), obliquus dorsalis I-II (Ob.d I: connects the epibranchial I and infrapharyngobranchial I; Ob.d II: connects epibranchial II and infrapharyngobranchial II) and medial obliquus dorsalis muscle (Ob.d.m; connects the infrapharyngobranchials) are muscles that serve the dorsal part of the branchial arches (Fig. 6).

Discussion

Ariosoma gilberti (Ogilby, 1898) lives in burrows on the flat sandy bottom of the continental shelf and feeds on mobile crustaceans, cephalopods and fishes. They are tail-first burrowers and emerge from their burrow at night to forage (Rosenblatt 1958; Asano 1962; Smith 1989). The immobile maxillary equipped with large pointed teeth, the caniniform and backwardly curved teeth of the mandibula, the large, pointed teeth of the anterior tip of the premaxillo-ethmovomer complex and an anterior moderate mouth gape of *A. gilberti* suggest grasping and impaling of elusive prey upon capture (Lauder 1980; Alfaro et al. 2001; Porter & Motta 2004). Combined with the large jaw closing muscles, they will assist in preventing escape during subsequent transport. Also, the large lateral and ventral bony

elements of the skull and associated muscles linked to the buccal cavity expansion and large opercular series in which is provided more room for the orobranchial cavity, suggest the presence of a hydraulic, suction-based mechanism as subsequent transport behavior in *A. gilberti*. In this mechanism, fishes transmit the piece or whole of the prey into the esophagus by hydraulic suction that is produced by depressing the mandible (Grubich et al. 2008).

In contrast, morays have evolved an alternative to this hydraulics based prey transport to move large prey from the oral jaws to the pharyngeal jaws (Mehta & Wainwright 2007). The pharyngeal jaws of morays can protract to deliver a second bite (Mehta & Wainwright 2007). Modification of the branchial arches in relation to the pharyngeal jaw functionality in muraenids has been described by Mehta & Wainwright (2008). In comparison to *A. gilberti* that still perform the hydraulic based prey transport, some cephalic features of muraenids including stout and robust neurocranial elements, elongated lower jaw as result of the posterior position of the quadrato-mandibular articulation, enlarged teeth of oral jaws and premaxillo-ethmovomer complex, reduction in the moveable cranial bones and their muscular connections, hypertrophied adductor mandibulae muscle complex, presence of the quadrato-maxillary and preoperculo-angular ligaments, connection of the quadrate to the A2 tendon of adductor mandibulae complex, caudoventral orientation of the fibers of large A3 section of adductor mandibulae complex may be considered as specializations to seize and devour large prey in relation to the presence of mechanical transport system.

The larger muscles of muraenids also need increasing the insertion site area (De Schepper 2007). Hence, muraenids with hypertrophied jaw muscles bear a large and elevated supraoccipital crest (Eagderi 2010), to increase the insertion site area for the jaw muscles. However, *A. gilberti* with smaller jaw muscle even lacks the supraoccipital bone. In addition, the reduction of the anterior part

of the suspensorium along with the lengthening of the pterospheneid in morays compared to that of *A. gilberti*, provides additional space for the large A3 section of morays.

The results of this study suggest that an innovative pharyngeal jaw apparatus, as present in morays, along with modified cephalic features compared to those of Bathymyrinae enabled the use of a mechanical transport system rather than a hydraulic one to pull prey into the esophagus (Mehta & Wainwright 2007) in order to allow an optimal performance of the cranial musculo-skeletal system.

Acknowledgments

The authors would like to thank M. McGrouther (Australian Museum) and R.S. Mehta for their valuable comments. This study was financially supported by Ghent University and the University of Tehran.

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